PALLIAL MARKINGS OF SOME PERMIAN SPIRIFERIDS

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(Plates XIII–XV)

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Synopsis

The pallial markings on a number of Permian spiriferids are described. Preserved pallial sinuses on specimens of *Subansiria*, *Trigonotreta*, *Sulciplica*, *Martinia*, *Notospirifer*, and *Ingelarella* suggest that these genera probably had pinnate vascular canals. The loci of setal follicles are preserved along the commissures of specimens of *Notospirifer*, *Ingelarella*, and *Subansiria*.

INTRODUCTION

Pallial markings of spiriferids are not often well preserved and in all of the specimens examined during a study of eastern Australian Permian spiriferids only a few displayed any evidence of the vascular system of the animal. It is the purpose of this paper to document the natures of these markings and to discuss briefly their relationships with the pallial systems of some other articulate brachiopods.

Reference to specimens housed in the collections of the Department of Geology of the University of Queensland and the Geological Survey of Queensland is by a number prefixed by the letters UQF and GSQF respectively. Localities indexed at these institutions are denoted by numbers following UQL and GSQL respectively.

PALLIAL MARKINGS OF SPIRIFERIDS

Pallial sinuses (mantle canals) of articulate brachiopods are extensions of the body cavity of the animal into the mantle (Hancock, 1859, p. 840; Williams, 1956, p. 272). In living articulate and inarticulate brachiopods the sinuses are the media of fluid circulation in the mantle (Morse, 1902, p. 352) and they serve as repositories for the genitalia (Williams, 1956, p. 272). Many of the terms used to identify the various types of sinuses and the degrees of their development were originally proposed by Öpik (1934) as a result of his study of the pallial markings of the clitambonitacids. Some additional names were added to Öpik's terms by Williams (1956) and Öpik's and Williams's terminologies are employed here.

Sinuses in the ventral valve of an articulate brachiopod arise from two areas in the valve. Those which originate medially in front of or in the field of muscular attachment are the vascula media, and those proliferating from the sides and the postero-lateral parts of the muscle field are the vascula genitalia. In the dorsal valve the vascula media and the vascula genitalia are again present but in addition there is sometimes a third pair of primary sinuses called the vascula myaria which arise midway between the vascular

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media and the vascula genitalia on each side of the valve (Williams, 1956, text figs. 6, 7). In both valves of the living articulate *Terebratulina* it is the posterior pair of pallial sinuses, the vascula genitalia, which contain the gonads, and in *Terebratulina* these sinuses are apparently more conspicuous than the antero-median pair of sinuses, the vascula media (Williams, 1956, pp. 272, 277, text fig. 7).

The arrangement of the pallial markings in spiriferids is best known from Williams's description of the mantle canals of *Athyris, Coelospira,* and *Meristina* (Williams, 1956, p. 279, text fig. 7). In both valves of *Athyris,* and in the dorsal and ventral valves of *Coelospira* and *Meristina* respectively all of the sinuses have a pinnate pattern. The mantle canals are narrow, are radially disposed, and are discrete for most of their length. They proliferate mainly by dichotomy but sometimes by trifurcation. The vascula genitalia in the ventral valves of *Athyris* and *Meristina* cover a larger area than the vascula media. Incorporation of the vascula myaria in the dorsal valves of *Athyris* and *Coelospira* is accompanied by a diminution in the area covered by the sinuses of the vascula genitalia. Only in the posterior part of the ventral valve of *Athyris* do the sinuses of the vascula genitalia coalesce into small structures reminiscent of the similarly placed gonad bearing pouches (gonocoels) of *Hemithyris* (Williams, 1956, text fig. 7).

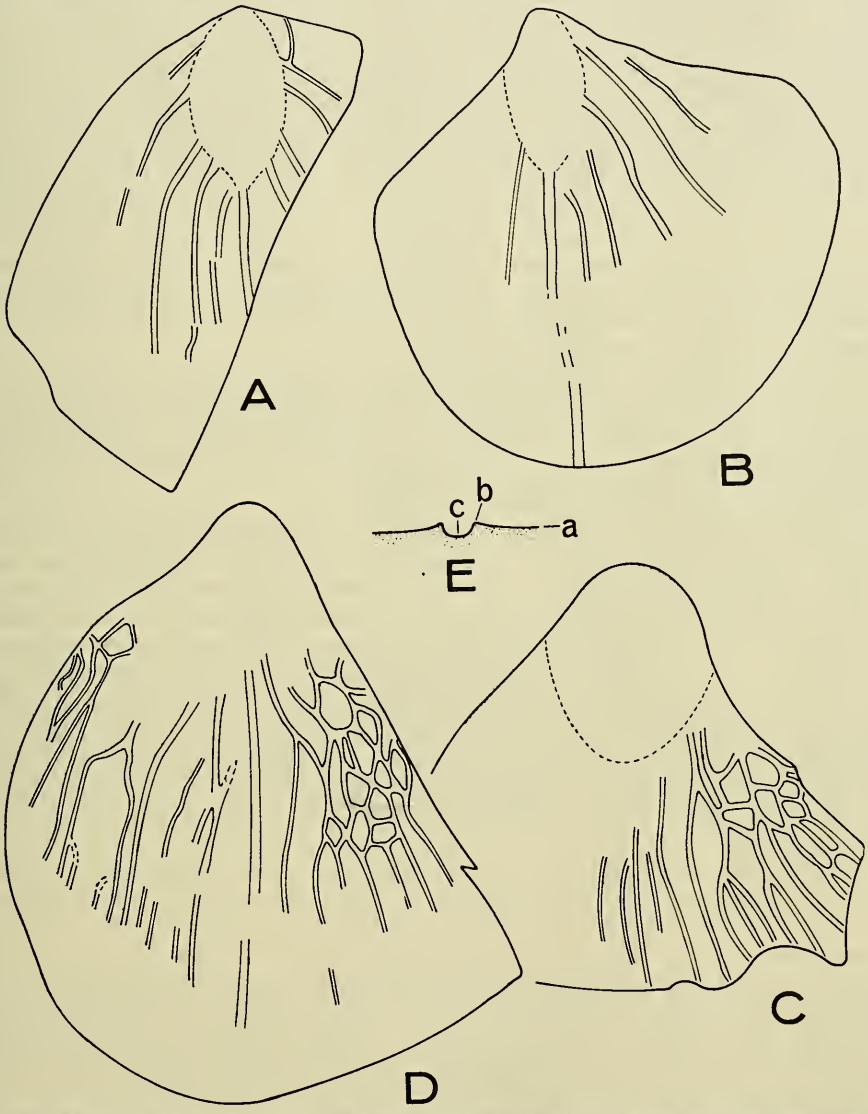
Similar conditions of the pallial sinuses prevail in the valves of *Atrypa reticularis* (Vandercammen and Lambiotte, 1962). The ventral vascula media are considerably abbreviated and Vandercammen and Lambiotte have suggested that the remaining pair of sinuses, which occupy most of the ventral valve, are the vascula myaria. Vascula myaria and vascula genitalia are present in the dorsal valve of *Atrypa reticularis* and, like the ventral vascula media of this species, the dorsal vascula media are much reduced. All of the markings are narrow linear strips which increase in number by branching.

George (1931, p. 113) described vascular markings in a species of *Martinia.* He noted that in the ventral valves of species of this genus there is invariably a strong centrally placed vascular canal which extends from the umbonal region to the anterior margin of the valve. Lateral canals radiate from the peripheries of the ventral muscle field and occasionally they dichotomize. In 1956 Williams (p. 279) stated that "traces of a pinnate condition in the pedicle valve at least are sometimes seen in members of the spiriferids and it is also found in species of *Brachythyris*". The vascular markings of a ventral of *Brachythyris elliptica* Roberts radiate from the muscle field and they may or may not dichotomize (Roberts, 1963, text fig. 11). Similarly in both valves of *Spirifer osbornei* Roberts there are narrow branching canals radiating from the peripheries of the areas of genital pitting (Roberts, 1964, pp. 207, 208). In the ventral valve of *S. osbornei* a narrow trunk arises from the front of the muscle field and runs towards the anterior margin. Waterhouse (1964, text fig. 53B) figured the vascular markings which are preserved on a specimen of *Martinia adentata* Waterhouse and he notes that the trunks "more or less radiate from the posterior part of the shell with few branches" (Waterhouse, 1964, p. 115). The vascular markings in the ventral valve of *Spinomartinia spinosa* Waterhouse (1968, pl. 9, fig. 7) also radiate from the peripheries of the field of muscular attachment.

The Permian spiriferids to be discussed here are *Martinia, Notospirifer, Ingelarella, Subansiria, Trigonotreta,* and *Sulciplica.*

Martinia: The pallial markings on the internal moulds of four ventral valves of *Martinia* sp. are shown in text figure 1 along with a diagrammatic cross section of the internal surface of the shell which would have underlain a

vascular canal (Pl. XIII, Figs. 1–4). The posterior parts of the primary pallial trunks overlie grooves in the shell that are flanked on each side by low ridges (Text fig. 1E), but towards the anterior of the shell the grooves underlying both primary and subsidiary trunks become shallower and the flanking ridges disappear.



Text figure 1. A, B, C, D, Camera lucida drawings of the pallial markings preserved on four ventral valves of *Martinia* sp. Specimens A, B, and C are illustrated in Plate 1, Figs. 2, 4 and 3. Specimen D is GSQF11575. E. Profile of the shell underlying a vascular canal: (*a*) internal surface of the shell, which is stippled; (*b*) small ridges which often border the pallial grooves; (*c*) pallial grooves, i.e., groove underlying vascular canal.

In the specimens depicted in Text figure 1A, B and D there is a prominent median trunk which extends from the area of muscular attachment to the anterior edge of the valve. This primary trunk is undivided in one of the

specimens (D), but in the other two (A and B) it seems that it may have given rise to at least one subordinate trunk just in front of the muscle field. The lateral sinuses are best preserved on the posterior halves of specimens A and B, and on the more anterior parts of specimens C and D. There appear to be four primary pallial trunks on each side of the median primary trunk in specimens A and B, and as far as these trunks can be traced they do not branch. The innermost pair of lateral trunks in specimen A is particularly prominent, and like the remaining lateral trunks, it arises around the periphery of the field of attachment of the muscles. The lateral trunks of specimens C and D yield a network (reticulum) of minor pallial sinuses on the shoulders of the interiors of the valves, and the sinuses which extend to the growing edge of the shell arise from the anterior sides of these reticula. In specimen D it seems that all of the lateral primary pallial trunks are involved in the formation of the reticulum of minor sinuses, suggesting that these vascular trunks are more closely related to each other than they are to the central pallial trunks and its subsidiaries. Possibly the latter are homologous with the vascula media of other living and fossil brachiopods and the former sets of pallial markings probably present the vascula genitalia.

The pattern of the pallial sinuses in the ventral valves of *Martinia* sp. is pinnate; no gonocoeles are present, but the vascular system seems to be composed simply of radially disposed or reticulate canals. Such reticula of ridges and pits occurring internally on the shoulders of articulate brachiopods are commonly referred to as genital markings.

Notospirifer: The preserved pallial markings of *Notospirifer* species consist of reticula of ridges and grooves on the internal surfaces of the valves in the umbonal cavities. The exact relationship between these markings and the vascular system of the animal is unknown, for no markings have been observed between these reticula and the marginal grooves which are common along the commissure of the shell. The latter grooves are radially disposed (Pl. XIV, Figs. 7, 8) and along the anterior commissure of the shell in Plate XIV, Fig. 7 they are about one millimetre apart. On the lateral parts of the commissural margin the grooves are more closely spaced. The grooves are best developed on the internal representations of the external inter-plical furrows. Similar grooves occur around the commissural margins of the shells of *Subansiria* and *Ingelarella*.

Ingelarella: Genital markings comprising reticula of ridges and pits occur on the internal surface of the shell in the umbonal cavities of both valves of species of *Ingelarella* (Pl. XIV, Fig. 4). The markings may or may not extend around the anterior limit of the muscle field in the ventral valve. From the anterior and lateral peripheries of the reticula, many narrow, equally sized grooves on the surface of the shell radiate towards the commissure (Pl. XIII, Fig. 5; Pl. XIV, Figs. 4–6; Pl. XV, Fig. 9). In one ventral valve the ridges comprising the reticula in each umbonal cavity seem to radiate from a point about midway along the side of the field of attachment of the muscles. When well preserved, the pallial grooves, like those on shells of *Martinia*, are bordered on each side by a fine ridge (Pl. XIV, Figs. 5, 6). Details of the manner by which the grooves (i.e., vascular canals) arise are not clear from the available specimens, but they seem to remain discrete after leaving the reticula of ridges in the umbonal cavities. As in *Notospirifer*, small grooves oriented perpendicular to the commissure, lie along the growing margins of the valves (Pl. XIII, Figs. 5–10). On some specimens each such marginal groove seems to be continuous with one of the pallial grooves which presumably underlay the vascular canals (Pl. XIII, Fig. 5; Pl. XIV, Figs. 5, 6; Pl. XV, Fig. 9).

Subansiria: The internal surface of the shell in each of the umbonal cavities is covered with a reticulum of ridges amongst which there are shallow pits (Pl. xiv, Figs. 1–3). Other pallial markings are generally not well preserved on specimens of *Subansiria,* although on the internal mould of one shell there are the traces of narrow grooves running towards the commissure from the genital markings (Pl. xiv, Fig. 1). The genital markings are present in both valves of the shell, and they extend from the peripheries of the fields of muscular attachment laterally almost to the cardinal extremities and forwards for up to one third of the length of the shell. Occasionally fine grooves like those along the margins of the shells of *Notospirifer* and *Ingelarella* are preserved along the commissure of a shell. Along the commissure of one specimen of *Subansiria* there are four marginal grooves along the internal surface of an external plication. These four grooves are about a half a millimetre apart.

Trigonotreta: The surfaces of the umbonal cavities in both valves of large specimens of *Trigonotreta* invariably bear reticula of ridges between which there are pits (Pl. xv, Figs. 3–8). Often the ridges and pits near the cardinal extremities are coarser than those bordering the fields of muscular attachment (Pl. xv, Fig. 3). The coarse lateral ridges seem to proliferate from a small number of coarse ridges, which run laterally along the cardinal margin from near the points of articulation of the valves. The more anteriorly located finer ridges diverge from an area between the coarse ridges and the anterior limit of the field of muscular attachment. In some ventral valves the reticula of ridges and pits completely encircle the field of attachment of the muscles (Pl. xv, Fig. 6). Unfortunately, in the shells of *Trigonotreta* there are no well preserved markings to indicate the nature of the vascular system between the umbonally located reticula of ridges and the periphery of the shell. In some valves there is a suggestion that equally-sized grooves radiate from the margins of the areas of genital markings (Pl. xv, Fig. 6). No marginal grooves are preserved on any of the studied shells of this genus.

Sulciplica: Prominent genital markings occur on the umbonal cavities of both valves of species of this genus (Pl. xv, Figs. 1, 2). On one specimen there are fine equally-spaced grooves and ridges radiating towards the commissure of the shell from the peripheries of the regions of genital markings (Pl. xv, Fig. 1). Whether it was the ridges or the grooves which were related to the vascular canals of the animal is unknown, and it is not clear exactly how the grooves and ridges are related to the genital markings.

Discussion

The reticula of ridges and grooves in the umbonal cavities of shells of *Martinia, Notospirifer, Ingelarella, Subansiria, Trigonotreta,* and *Sulciplica* comprise what are commonly called genital markings. The pallial grooves of shells of *Ingelarella, Subansiria,* and *Sulciplica* would seem to have radiated from the peripheries of these areas of genital markings. The markings in the umbonal cavities of some of the above genera differ from those of *Martinia.* Whereas grooves on the internal surface of the shell comprise the reticula in *Martinia,* it is ridges which form the reticula in *Subansiria, Trigonotreta,* and *Sulciplica.* In *Martinia* the pallial grooves underlying the vascular canals each arise directly from the reticulum of grooves (Text fig. 1). On the other hand in *Subansiria, Trigonotreta,* and *Sulciplica* it is uncertain whether it is the ridges or the pits of the reticula which underlay the components of the vascular system.

The distribution of the pallial markings of *Ingelarella, Subansiria,* and *Sulciplica* suggests that the vascular canals of these genera may have had a pinnate pattern. Vascular media and vascula myaria are not physically distinguishable in the dorsal valves of any of the specimens examined. It has already been suggested that the lateral sinuses in the ventral valves of *Martinia* are the vascula genitalia, and that the commonly observed quite prominent median canal comprises the vascula media. No prominent median groove has been observed in the ventral valves of *Notospirifer, Ingelarella, Subansiria, Trigonotreta,* or *Sulciplica* and as Roberts (1964) suggested for similar markings in *Spirifer osbornei,* the preserved pallial markings in the shells of these genera probably represent the vascula genitalia. In some specimens of *Trigonotreta* there are coarse posterior and postero-lateral genital ridges and finer anterior ridges. This apparent division of the genital markings occurs in both dorsal and ventral valves of *Trigonotreta* but its significance is unknown.

According to Rudwick (1965, p. H204) the setae along the growing margins of the valves of *Terebratulina* correspond in position to the external costellae, although not all costae in living brachiopods correspond to a single seta. Williams and Rowell (1965, p. H81) note that the setal follicles of the living genus *Hemithyris* occur at regular intervals along the mantle edge irrespective of the plications of the shell. On the internal surface of the shell of *Hemithyris* slight ridges separate the follicles so that each follicle is located in a small groove. The small radially aligned grooves occurring along the growing margins of the valves of *Notospirifer* and *Ingelarella* each probably represent the location of a setal follicle (Pl. xiii, Figs. 6–10). The grooves vary from being one half of a millimetre to two millimetres apart. In some specimens of *Ingelarella* each marginal groove seems to be continuous with a groove of the system of radial markings suggesting that each vascular canal led to a setal follicle (Pl. xiii, Fig. 5; Pl. xiv, Figs. 5, 6; Pl. xv, Fig. 9).

In enteletaceans Williams and Wright (1963) and Kemezys (1968) suggest that each costa on the shell represents the location of a setal follicle at the growing margin of the shell. Each setal follicle of *Notospirifer* and *Ingelarella* was not confined to the internal representation of a plica on the shell. Rather the follicles were more or less uniformly distributed along the commissure of the shell. On one specimen of *Notospirifer* there are more follicles per unit distance along the lateral portions of the commissure than there are along the anterior parts of the commissure. On this specimen several follicular grooves occur along the internal surface of each external plication.

In the spiriferids studied here there is no evidence to indicate that the pallial trunks radiating from the genital markings were confined to individual plicae as Kemezys suggests for entelectaceans. Indeed, on the smooth or broadly plicate spiriferid genera the preserved markings indicate that uniformly distributed, radiating, equally-sized vascular canals were present throughout the mantle. However, complete details of canals of the studied genera are unknown, and in multi-ribbed genera such as *Trigonotreta* it may eventually prove that there is a relationship between the quite small plications of the shell, the vascular canals, and the setal follicles at the growing margins of the shell.

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EXPLANATION OF PLATES

PLATE XIII

Figs. 1–4. *Martinia* sp. Internal moulds of four ventral valves showing the impressions of the pallial markings on the internal surfaces of the shells. X1½. GSQF11344, GSQF11343, GSQF11342, and GSQF11345 respectively, all from the Oxtrack Formation at GSQLD211.

Fig. 5. *Ingelarella* sp. Internal mould of dorsal valve showing pallial sinuses radiating from the medio-posterior part of the valve. X1. UQF57496 from the Ulladulla Mudstone at UQL3152.

Figs. 6, 7. *Ingelarella* sp. 6, Internal mould of dorsal valve showing the fine radially disposed grooves around the commissure of the shell. X1. UQF59131 from the Branxton Formation at UQL3258. 7, An enlargement by 3 of part of Fig. 6.

Figs. 8–10. *Ingelarella profunda* Campbell 1961. 8, Latex cast of the external mould in Fig. 10. X3. 9, Same cast as in Fig. 8. X1. 10, Internal mould of a ventral valve. X3. UQF59132 from the Tiverton Formation at UQL3127.

PLATE XIV

Figs. 1–3. *Subansiria* sp. Internal moulds of a ventral valve and two dorsal valves respectively, which show the pallial markings in the posterior parts of the valves. 1, X2. UQF59133. 2, X1. UQF59134. 3, X2. UQF52867. All specimens are from the Tiverton Formation at UQL3127

Fig. 4. *Ingelarella ovata* Campbell, 1961. Internal mould of a ventral valve showing the pallial sinuses diverging from the medio-posterior part of the valve. X1½. UQF59135 from the Tiverton Formation at UQL3127.

Figs. 5, 6. *Ingelarella ovata*. Two views of the same dorsal valve to show the pallial markings. X2. UQF59136 from the Tiverton Formation at UQL3127.

Figs. 7, 8. *Notospirifer hillae* Campbell, 1961. Internal mould of a shell showing the impressions of the setal grooves along the commissural margins of both of the valves of the shell. X2. UQF59137 from the Tiverton Formation at UQL3127. 8, Latex cast from part of the specimen in Figure 7. X2.

PLATE XV

Fig. 1. *Sulciplica stutchburii* (Etheridge, 1892). Internal mould of a ventral valve showing the impressions of the genital markings from which arise the pallial sinuses. X2. UQF59138 from the Tiverton Formation at UQL3127.

Fig. 2. *Sulciplica transversa* Waterhouse, 1968. Internal mould of a ventral valve showing the impressions of the pallial markings in the posterior part of the valve. X1. AMF14014 from Bundanoon Gully, 2 miles south of Bundanoon Railway Station, New South Wales.

Fig. 3. *Trigonotreta stokesi* Koenig, 1825. Postero-dorsal view of a complete internal mould. X1. UQF59139 from the Tiverton Formation at UQL3127.

Fig. 4. *Trigonetreta* sp. Interior of the medio-posterior part of a ventral valve showing the pallial markings marginal to the field of muscular attachment. X1. UQF49147 from the Bundella Mudstone at UQL3050.

Fig. 5. *Trigonotreta stokesi.* Dorsal view of a complete internal mould. X1. UQF59219 from the Tiverton Formation at UQL3127.

Fig. 6. *T. stokesi.* Latex cast from an internal mould of a ventral valve. Anastomosing ridges surround the field of muscular attachment. X2. UQF59216 from the Tiverton Formation at UQL3127.

Fig. 7. *T. stokesi.* Postero-ventral view of the internal mould of a ventral valve. X1. UQF21072 from the Tiverton Formation.

Fig. 8. *T. stokesi.* Latex cast from the internal mould of a ventral valve. Pallial markings comprising a reticulum of ridges surround the field of muscular attachment. X2. UQF59140 from the Tiverton Formation at UQL3127.

Fig. 9. *Ingelarella angulata* Campbell, 1959. Dorsal view of a complete internal mould showing pallial markings. X1. UQF49764 from the *Fenestella* zone in the Branxton Formation at UQL2796.